

Extreme climate events and wet grasslands: plant traits for ecological resilience

Sarah J. Brotherton · Chris B. Joyce

Received: 26 July 2014 / Revised: 21 November 2014 / Accepted: 24 November 2014 / Published online: 10 December 2014
© The Author(s) 2014. This article is published with open access at Springerlink.com

Abstract Extreme climate events, including floods and droughts, represent disturbances that impact plant functioning, biodiversity and ecosystem processes. Wetlands can mediate climate change impacts through their multiple ecosystem services, and wet grasslands offer a fascinating wetland case because they are adapted to regular disturbance regimes typified by inundation, cutting and/or grazing. This review identifies key concepts for a better understanding of extreme climate impacts on wet grassland plant communities, focussing upon the use of functional traits for ecological resilience. It suggests that wet grasslands are underrepresented in extreme climate event experiments, despite some field studies that show floods have significant impacts upon community composition. Mechanisms for ecological stability and resilience are linked to functional diversity through plant traits, via niche complementarity or dominance. Facilitation may be important as climate stresses increase, while modified plant behaviour may promote recovery. However, plant community responses to extreme events are complex; the challenges for wet

grassland researchers include: (i) identifying thresholds, tipping points and lag effects; (ii) monitoring key community components; (iii) using effective plant trait metrics; (iv) investigating beyond conservative norms; (v) combining multiple stressors and traits and (vi) extrapolating experimental results to field conditions.

Keywords Climate change · Disturbance · Drought · Flood · Stability · Wetland

Introduction

Most climate change science has focussed upon long-term trends, averages and gradual changes. Consequently, while the effects of climate trends on many ecosystems have been assessed (e.g. Ramsar, 2002; IPCC, 2013) similar heightened understanding of extreme climate events caused by climate change is lacking. Extreme events tend to be defined either with an emphasis on climate variability, notably the rarity of such events, or on the atypical environmental responses that follow climate extremes. For example, Smith (2011a) defines extreme events as those defined by great magnitude over short temporal scales that may cause profound ecosystem responses, often disproportionately greater than those predicted under steady change scenarios. They include intense precipitation and extreme temperatures, and consequent

Guest editor: Koen Martens / Emerging Trends in Aquatic Ecology

S. J. Brotherton · C. B. Joyce (✉)
School of Environment and Technology, University of Brighton, Cockcroft Building, Lewes Road, Brighton BN2 4GJ, UK
e-mail: c.b.joyce@brighton.ac.uk

floods, heat waves, wildfires and droughts. The IPCC (2012) describe extreme climatic events as statistically rare (90th percentile or above), at the extreme end of climate variables. From an ecological perspective, climate events can be considered a disturbance that impacts plant functioning, biodiversity and ecosystem processes. Globally, extreme weather or climate events are expected to become more frequent and increase in intensity and duration (IPCC, 2007) and the latest assessment highlights the significant vulnerability and exposure of some ecosystems to climatic variability (IPCC, 2014). The need for greater understanding of the environmental and ecological impacts of extreme climate events is, therefore, pressing (Jentsch et al., 2007; Smith, 2011a; Reyer et al., 2013; Niu et al., 2014), especially as society seeks to adapt to climate change and its effects.

Wetlands including wet grasslands may have a role to play in mediating some consequences of extreme events by providing ecosystem services such as water storage, sediment and pollution removal, and flood attenuation. Wet grasslands also support important biodiversity and cultural services, including internationally important plant and bird communities and vital agricultural production through grazing and hay cutting. The quality of such services is reliant on the functional diversity within ecosystems (Díaz & Cabido, 2001; Isbell et al., 2011). In particular, diversity of plant functional traits within communities is an important contributing factor in ecosystem processes and services. Wet grasslands provide an interesting case for elucidating extreme climate event impacts because they are widely distributed, show geographical variation but have key vegetation, hydrological and management features in common. They are ecotonal wetlands, transitional between aquatic and terrestrial ecosystems, maintained in a dynamic equilibrium by regular disturbance (i.e. agricultural management, periodic inundation), which often supports high diversity and rare species, but are responsive to hydrological fluctuations (Toogood et al., 2008; Berg et al., 2012). They may, therefore, either provide early warning of potential ecosystem change, especially as diverse wet grasslands can allow small or rapid responses to be discriminated (Joyce, 2001), or show resilience to extreme events through existing adaptations to a dynamic environment. They are also easier to study or sample than many other wetlands, such as those dominated by trees and/or continuously

inundated or waterlogged. Moreover, extreme events may have particularly important consequences for wet grassland stakeholders, as they can prevent or delay vital management activities such as hay cutting or livestock grazing, leading to loss of income or nature conservation benefits.

This review identifies key concepts and theories shaping ecological understanding of the impacts of extreme climate events on plant communities. It focusses upon the use of plant traits to indicate ecosystem functioning and resilience in order to provide insights for future climate change research in wet grassland environments.

Extreme climate events

Easterling et al. (2000) suggest that the natural environment is strongly affected by extremes in climate and weather, and cites numerous examples in the literature, where one-off extreme events have changed the body size, sex ratio and initiated population crashes in animal populations, and initiated turnover in plant communities. Extreme climate events are measured by both direct and indirect impacts, because the term implies a physical manifestation in time and space. Direct events include extreme temperatures or precipitation, while indirect effects range from drought and fire, increased incidence of heat waves, to flooding as a consequence of changes in precipitation patterns. Direct and indirect events are often conflated in the literature, as indicated by the number of references to severe floods as extreme events (Meehl et al., 2000; Jentsch et al., 2007; Smith, 2011a) despite these being an indirect effect of intense precipitation. Extreme climate events are notable by both their magnitude (great) and duration (short) in comparison to average climate means (Jentsch et al., 2007; Planton et al., 2008) which mean they fall outside normal weather variables (Meehl et al., 2000). Because of this, the effect on the environment is not proportional to their temporal distribution (Jentsch et al., 2007) and, therefore, it is possible to appreciate extreme climate events as weather events that may drive change through both occurrence and response. Consequently, when considering likely ecosystem impacts, extreme climate events are probably more important than climate trends (Meehl et al., 2000; Tebaldi et al., 2006; Jentsch et al., 2007; Smith, 2011a; Reyer et al., 2013; Thompson et al., 2013), particularly as the environmental response

to an extreme event is in itself often sufficient to drive a change in ecosystem functioning (Gutschick & BassiriRad, 2003; Smith, 2011a). This may prompt a more rapid response than increasing mean trends, suggesting that extreme events accelerate climate change effects (Jentsch et al., 2007).

Some extreme events are expected to increase in frequency and duration in response to the changing climate (Zwiers & Kharin, 1998; Tebaldi et al., 2006; Planton et al., 2008; IPCC, 2012). Heat waves have become more frequent in Europe, Asia and Australia, and extreme precipitation events have increased in North America and Europe (IPCC, 2013). Globally, an increase in extreme precipitation events is predicted, particularly in the temperate and boreal regions of both hemispheres (O’Gorman & Schneider, 2009a), although models are less robust for precipitation than they are for temperature (Orlowsky & Seneviratne, 2012). When precipitation models are compared to observations the models appear to be underestimating extreme events, which indicates that future extreme rainfall may be more intense than current predictions suggest (Fowler & Wilby, 2010). Predicting when an actual event is likely to occur is difficult (IPCC, 2007; O’Gorman & Schneider, 2009b) and, even though extreme events are not random, it is not always possible to forecast them. Extreme precipitation and other weather extremes are often attributed to changes in global atmospheric conditions at locations distant from the event (O’Gorman & Schneider, 2009a; Trenberth & Fasullo, 2012). Clustering of extreme events has been observed to occur; for example 2010 witnessed extreme precipitation, flooding, drought and heat waves across both hemispheres within a six month period (Trenberth & Fasullo, 2012). Predicting the risk of extreme flooding is particularly complex, although Milly et al. (2002) suggest a doubling of 100 years flood events over the twenty first century in large (+200,000 km²) river basins. However, Kundzewicz et al. (2005) suggest that predicted increases in flooding are not linked to climate but rather to changes in land management and increased development on sites at risk of flooding.

Wet grasslands and climate change

Wet grasslands are biologically diverse wetland components of agricultural landscapes that provide multiple

ecosystem services, including flood attenuation, groundwater recharge, sediment storage, nutrient removal, erosion protection and aesthetic value (Joyce and Wade, 1998). The wet grassland communities included in this review are semi-natural, formed by drainage of other wetland types (e.g. fens or marshes) or forest clearance on floodplains, and have been maintained for centuries by human intervention, often cutting for hay or extensive grazing by livestock. As suggested by Grime (1979), this intermediate level of disturbance promotes maximal diversity as it removes dominants, allowing many species to co-exist (Fig. 1). Wet grasslands have an abundance of grasses (or sedges), periodic flooding with fresh or brackish water, or a high water table for at least some of the year, sufficient to influence the vegetation and associated biological diversity. Nevertheless, wet grassland plants possess attributes to survive flood events that would compromise survival of many terrestrial species, including adventitious roots and aerenchyma to overcome hypoxic waterlogged soils and the ability to continue photosynthesis even when submerged (Blom & Voeselek, 1996). Wet grassland types include wet meadows and pastures, floodplain, riparian or alluvial grasslands, coastal grasslands, polders, fen grasslands and wet prairies. The extent and status of wet grasslands is not well known beyond the regional or occasionally national level, partly due to inconsistencies with defining the various types. However, it is likely that the species-rich, ancient wet grassland resource focussed upon in this paper experienced areal losses of at least 80% during the

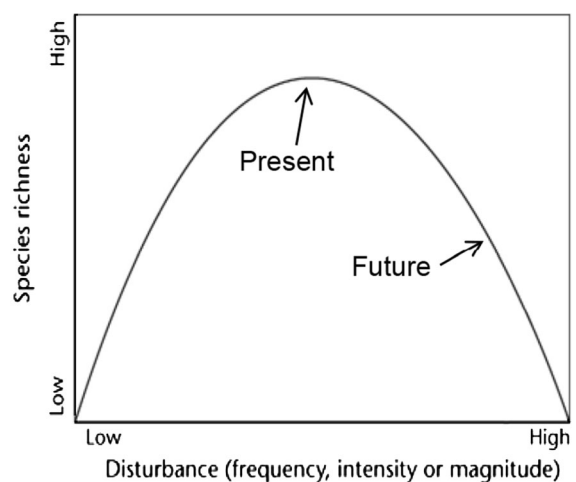


Fig. 1 Wet grassland species diversity model with a present and future disturbance scenario in which extreme climate events increase. The model is based upon Grime (1979)

twentieth century, mostly due to drainage and agricultural changes (Joyce, 2014).

Projections of climate effects on wetlands are generally not well understood (Erwin, 2009) due to the complexity of many wetland systems. This is especially the case for wet grasslands, despite their cultural, biodiversity and ecosystem service values. The greatest impact of climate change is likely to be any change in water quantity, thereby affecting wet grassland hydrology. Some of the most significant extremes affecting hydrology are likely to be the increased length or number of heat waves and droughts, intense precipitation events, and extreme coastal high water levels and storms (Table 1). Altered hydrology will be a serious stressor on wet grassland environments, along with saline intrusion, erosion, sedimentation and fire (Table 1), while multiple stressors may interact to compound climate extreme impacts. More specifically, wet grasslands may be particularly sensitive to: changes in precipitation patterns leading to insufficient water at the peak vegetation period, or increased recharge, erosion and/or sedimentation under extreme precipitation; saline intrusion from storm surges; loss of feeding and breeding habitats important to wading birds and water fowl; enhanced productivity under increased

precipitation in certain regions (Ramsar, 2002); loss of biodiversity, and increases in invasive species (Erwin, 2009). For plants, climate change may be expected to affect productivity, diversity, phenological timing and carbon dioxide take up, altering biogeochemical processes (Easterling et al., 2000; McCarty, 2001; Smith, 2011b; Reyer et al., 2013). Plant responses may be either positive or negative and will modify competitive relations between species, which may be crucial in wet grasslands, where a diversity of perennial species co-exist.

A combination of decreasing rainfall and higher temperatures predicted under many climate change scenarios is likely to exacerbate deficits in water budgets for many temperate wet grasslands through increased evaporation and evapotranspiration (Dawson et al., 2003; Thompson et al., 2009; Acreman et al., 2009). A model of floodplain dynamics under different emissions scenarios predicts that the number of shallow flood events in the UK would decrease by up to 90%, because of reductions in available water (Thompson et al., 2009). Therefore, some wet grassland species are expected to migrate northwards as a result of increased temperatures reducing water tables (Dawson et al., 2003), potentially resulting in the loss of dominant functional species, which may affect ecosystem processes. Reduced water supply could initiate a negative feedback loop, where the wet grassland would be unable to recover, favouring a more terrestrial community composition (Čížková et al., 2013) and leading to changes in nutrient cycling, decomposition, soil microbes and primary production (Öquist & Svensson, 1996). In some regions, such as southeast Europe, higher temperatures and increased aridity will lead to wet grasslands becoming sub-halophytic, where evaporation of water causes a high concentration of salts in the soil (Eliáš et al., 2013). However, overall wet grasslands and other wetlands reliant on river inflows or groundwater are predicted to be less affected by climate change than those wetlands directly dependent on precipitation, such as bogs (Öquist & Svensson, 1996; Brinson & Malvárez, 2002; Acreman et al., 2009).

Extreme climate events could disrupt the functioning of wet grasslands especially if they are ‘so amplified, reduced, or mistimed that they produce significant changes...’ to species populations and habitats above critical thresholds (Sparks et al., 1990). Unseasonal inundation, such as summer flooding in

Table 1 Climate change extremes and stressors likely to impact wet grasslands

Extremes	Stressors
Increased length or number of heatwaves	Altered hydrology (e.g. flooding, drought, increased evapotranspiration, increased abstraction)
More intense and longer droughts	Fire
Increased number of intense precipitation events	Sedimentation
Increased extreme coastal high water	Salinity
Possible increased storm activity	Erosion
Possible increased flooding	Increased production
Possible interactive effects (e.g. high salinity)	Loss of food resources, e.g. for birds
	Vectors for invasive species and disease
	Heat stress on wildlife

Adapted from Ramsar (2002) and IPCC (2012)

temperate wet grasslands, has already been observed to induce plant community, soil nutrient and biodiversity impacts (Burgess et al., 1990; Antheunisse & Verhoeven, 2008). Anthropogenic impacts may magnify climate effects on wet grasslands. This may be especially the case for modified grasslands with low species diversity, such as those improved for intensive agriculture, as loss of key species reduces the functioning of ecosystems and ultimately degrades its service use (Díaz et al., 2006). Degraded grasslands may already be functionally extinct (Erwin, 2009), leaving them more vulnerable to multiple climate impacts (Gitay et al., 2011) if their ability to recover has already been compromised.

Plant community concepts

Plant traits and functional diversity

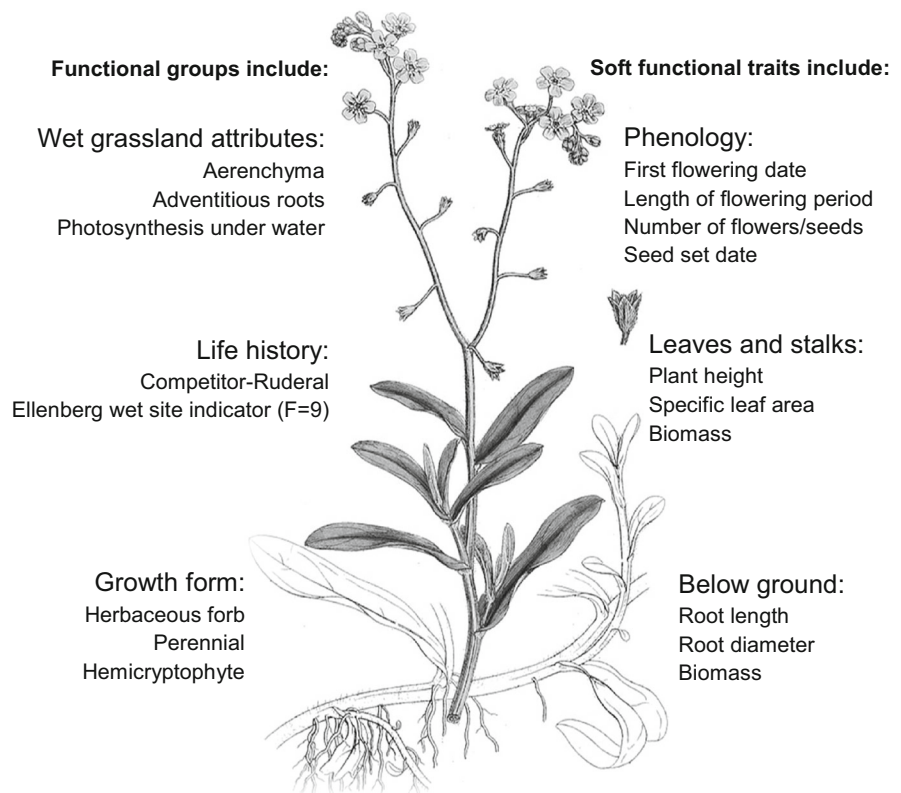
Plant functional traits are rapidly becoming the currency by which community structure and functioning is measured. Plant traits are the characteristics of a particular species, including species morphology, phenology, physiology and behaviour (Díaz & Cabido, 2001) and are adaptations to particular environmental conditions, developed through pressures on reproduction, growth and survival (Violle et al., 2007). Traits are, therefore, not randomly distributed but are accorded through the abiotic and biotic conditions under which a species survives (Lavorel & Garnier, 2002). Diversity is also now increasingly measured by functional groups, traits and genetic diversity (Cadotte et al., 2009). This is known by the overarching term functional diversity (Cadotte et al., 2011). Functional groups (also referred to in the literature as types or guilds) are groups of species for which responses to environmental factors can be clustered or ranked, but are not necessarily genetically related (Boutin & Keddy, 1993). Groups may also be classifications which have one dominant trait in common. Examples in wet grasslands include legumes, herbs or forbs (all non-woody flowering plants not including grasses), competitors and ruderals, Ellenberg's indicator values for moisture, and annuals and perennials (Toogood et al., 2008; Toogood & Joyce, 2009). Examples of functional groups pertaining to *Myosotis scorpioides*, a widespread plant of wet grasslands and other

wetlands, are shown in Fig. 2. There is no common consensus on groups (Lavorel et al., 2007), probably because functional groups can be site, context and investigation specific. In the context of this review functional diversity includes traits and groups and but not genetic diversity as functional traits are phenotypic rather than phylogenetic (Loreau & Behera, 1999).

The collection of functional diversity data may be considered more important than other measures of species diversity, such as richness, because of the close association with ecosystem functioning (Díaz & Cabido, 2001; Cadotte et al., 2011). Ecosystem functions related to biogeochemical processes, ecosystem services, resilience to disturbance and long-term stability in a community have all been closely allied to functional diversity (Loreau, 2000; Hooper et al., 2005; Díaz et al., 2007; Byun et al., 2013; Butterfield & Suding, 2013). This indicates that plant traits and functional groups are a powerful tool for assessing community responses to, and effects of, perturbation such as through extreme climate events. A further advantage of traits over species richness is the universality of traits (Díaz et al., 2004; Norberg, 2004; Araya et al., 2010). Hypothetically, predictions could be made regarding likely community responses globally, where comparable environmental conditions allow similar traits to prevail even when species differ. Established wet grasslands should represent an excellent case to test functional traits globally because they are widely distributed and are defined by key features held in common, namely an abundance of grasses (or sedges), a diversity of herbs, periodic flooding or a high water table, and regular vegetation management.

Functional plant traits can be categorised as soft or hard. Soft traits include those that are easily measurable for wet grassland plants (Fig. 2), such as biomass, phenological timing, plant cover, growth form, leaf life span and seed mass (Table 2; Weiher et al., 1999) and are more often used as measures of response. Hard traits include carbon fixation, gas exchange, photosynthetic rates and nitrogen capture (Table 2), and are more important when considering effects on ecosystem processes (Lavorel & Garnier, 2002). Soft traits (Sherry et al., 2007; Jentsch et al., 2009) and functional groups (White et al., 2000; Beltman et al., 2007; Jentsch et al., 2009; Arnone et al., 2011) are more commonly used than hard traits to investigate extreme climate events (Table 2). However, hard

Fig. 2 Examples of functional groups and soft traits for *Myosotis scorpioides*, a widely distributed plant species of wet grasslands and other wetlands. Functional groups are known attributes that can be used to classify wet grassland plants. Soft functional traits are measurable and can be used as indicators of environmental response, e.g. to disturbance



traits are often measured alongside either soft traits or biomass in grasslands (Jentsch et al., 2011; Dreesen et al., 2012). Table 2 summarises the characteristics of experiments used to measure extreme climate events and shows that most studies involve dry grassland forbs and grasses, especially in response to high temperature and drought treatments. Wetlands are underrepresented, although field studies on actual high magnitude flood events have been published for floodplain grasslands (e.g. Vervuren et al., 2003; Ilg et al., 2008) and indicate mixed impacts upon biodiversity. The effects of extreme droughts have also been studied in the field, especially on woodland or shrub communities (Valladares & Niinemets, 2008; Cavin et al., 2013; Herrero & Zamora, 2014), and Koyama & Tsuyuzaki (2013) studied seedlings of perennial herbs in a peatland affected by extreme drought. In general, extreme climate events have been found to provoke a complex array of community responses that have been considered both positive (e.g. increased productivity) and negative (e.g. mortality), dependent upon the type and timing of event, plant community composition and resilience to recurrence.

Mechanisms for plant community resilience

Resilience is the flexibility within a system that allows it to recover from a disturbance to a previous functioning state (Mori, 2011). Stability, therefore, encompasses resilience (Loreau & Behera, 1999), because resilience is a part of the functioning of a stable community, as defined by community persistence and consistency through time and space (Grimm & Wissel, 1997). Figure 3 illustrates the mechanisms of plant community responses to disturbance imposed by extreme climate events. There are several key theories proposed to explain how plant communities manifest stability and resilience to disturbance. Wet grasslands are maintained by a regular disturbance regime in a form of dynamic equilibrium, within which the community is adapted by means of specific plant traits. This implies a system of stability in which the dominant traits and diversity flex dependent upon environmental factors, allowing the most suitable species to replace others through ‘complex adaptive strategies’ as environmental conditions change (Norberg, 2004). Adaptive strategies explain how a

Table 2 Examples of plant functional traits used for measuring responses to extreme climate events in experiments

Reference	Habitat	Species	Climate event type	Soft traits	Hard traits
Walter et al. (2011)	Agricultural grassland	Single grass species	Recurrent drought	Above-ground biomass	Relative leaf water content, leaf gas exchange
Jentsch et al. (2011)	NW European grass and heathland	Grasses and forbs	Drought and/or precipitation	ANPP, plant cover, below-ground biomass, shoot-to-root ratio, senescence, phenological timing	Leaf water potential, gas exchange, photosynthetic light conversion, leaf C and N isotope, leaf C:N ratio, leaf protein content
Jentsch et al. (2009)	NW European grassland	Grasses, forbs and soil microbes	Drought prolonged over 5 years	Phenological timing	–
Kreyling et al. (2008)	NW European grass and heathland	Grasses and forbs	Drought and/or precipitation	ANPP, tissue die-back	–
Sherry et al. (2007)	Tall grass prairie	Grasses and forbs	Heat and double annual precipitation ^a	Phenological timing, life-form	–
Arnone et al. (2011)	Tall grass prairie	Grasses and forbs	Heat	ANPP, life-form, photosynthetic pathway	–
Peñuelas et al. (2004)	NW European and Mediterranean shrubland	Ericaceous shrubs	Warming and drought ^a	Plant growth, cover, biomass, flowering plants and shoots, herbivory damage	14C fixation, plant and litter chemical composition
Fay et al. (2003)	Great plains grassland	C4 grasses	Precipitation reduced by 30% and dry periods by 50% ^a	ANPP, root biomass	–
Dreesen et al. (2012)	W European grasslands	Three forb species	Drought and/or heat	Biomass, relative green plant cover	Light-saturated photosynthetic rate and stomatal conductance
Dreesen et al. (2013)	W European grasslands	Three forb species	Recurrent drought and/or heat	Plant and leaf survival, leaf colour, biomass	–
De Boeck et al. (2011)	NW European grasslands	Three forb species	Drought and heat	Biomass, vegetation height	Gross photosynthesis
White et al. (2000)	Agricultural grassland	Grasses and forbs	Heat ^a	Photosynthetic pathway, life-form, biomass	–
Vervuren et al. (2003)	NW European floodplain	Four forb species	Flooding	Plant survival	–
Reusch et al. (2005)	Sea grass meadow	One Eelgrass species	High water temperature ^a	Biomass, shoot number	Genotyping

ANPP above-ground net primary productivity

^a Not specifically defined as extreme in the publication

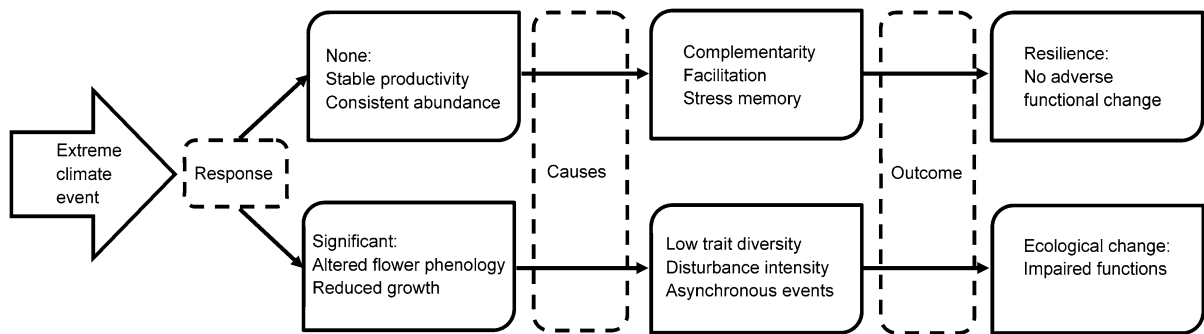


Fig. 3 Scheme representing examples of contrasting responses, causes and outcomes to extreme climate events by plant communities

community resists disturbance that would otherwise destabilise it and prompt fundamental community change, potentially to an alternative stable state (Beisner et al., 2003). For example, disturbance can modify the growth strategies of species as they respond to changes in habitat or competitors. Communities already adapted to dynamic environmental factors, such as wet grasslands functioning within variable hydroperiods and cutting or grazing disturbance (e.g. floodplain grasslands), could resist and/or recover from extreme climate events through adaptive strategies if response thresholds are not exceeded.

Complementarity and the mass ratio hypothesis can be linked to functional diversity through the distribution of traits (Díaz et al., 2007). The niche complementarity theory suggests that it is species diversity and, therefore, the corresponding diversity in traits that stabilise a community (Loreau et al., 2001) because niche overlap through partitioning prevents functional loss even if particular species are extirpated. Berg et al. (2012) proposed that such compensatory dynamics explained the greater resistance of diverse Estonian coastal wet grasslands to reinstated cutting management compared to species-poor wetlands. In practice, species and trait diversity should be regarded separately as subordinate species may make a proportionally larger contribution to the functioning of ecosystems than would be expected (e.g. from biomass) compared to dominant species (O’Gorman & Emmerson, 2009; Gibson et al., 2013). This may be particularly important for wet grasslands, where plants of small stature contribute substantially to species richness and nature conservation value (e.g. orchids) and are highly sensitive to environmental change, for example being amongst the first lost after fertilisation

(Joyce, 2001) or abandonment (Joyce, 2014). The Mass Ratio Hypothesis supposes that the dominant species by biomass support the overriding traits that stabilise the community (Grime, 1998), therefore, a community does not require high species diversity to function. This has not been explicitly tested in wet grasslands, but is potentially highly relevant for many wet grassland communities dominated by productive grasses, large sedges or robust herbs such as *Filipendula ulmaria*. In general, complementarity is fundamental in explaining stability and resilience in highly diverse systems (Fig. 3; Cardinale et al., 2007; Steudel et al., 2011). However, increased trait diversity cannot be assumed to always be associated with community stability (Loreau & Behera, 1999). For example, less diverse heathland plant communities were better able to withstand simulated extreme climate events compared to more complex compositions in experimental plots (Kreyling et al., 2008).

Stability, particularly under high or multiple stressors, may also be achieved through plant–plant facilitation (Fig. 3). Reproduction, growth and survival can all be enhanced by facilitation through modification of the immediate environment by a neighbouring plant of a different species, and is commonly associated with stressed biomes such as tundra and arid environments (Brooker et al., 2008) as well as coastal wetlands (Zhang & Shao, 2013). There is also some evidence of facilitation occurring in less severe habitats that undergo an extreme climate event, including Mediterranean shrubland subjected to extreme drought (Lloret & Granzow-de la Cerda, 2013) and grasslands affected by extreme drought and rainfall (Kreyling et al., 2008). These examples appear to support the stress-gradient hypothesis that suggests

that as environmental stresses increase plant interactions shift from competitive to facilitative (Bertness & Callaway, 1994). The role of facilitation in wet grasslands is unclear, but it may enable plant communities to persist in the face of extreme events such as droughts and floods, especially as terrestrial and wetland species co-exist uniquely in wet grasslands.

The theory of ecological stress memory suggests a plant may modify future behaviour following a stressful event, thereby making it more resilient to future extremes (Fig. 3; Walter et al., 2013). This was observed where grassland maintained productivity after repeated and worsening droughts year-on-year (Fay et al., 2003), although the concept has not yet been tested in wet grasslands, where floods and droughts represent the most likely stressful events. Effectiveness of stress memory can vary temporally, as the longer the time between extreme events the more likely a plant is to be resilient (Dreesen et al., 2013). This is an important consideration as extreme climate events are predicted to increase in frequency as well as intensity and duration. If a plant or population does not recover sufficiently after an extreme event it may increase sensitivity to any recurring events (Lloret et al., 2004), as indicated by observations of frequently inundated coastal and floodplain wet grasslands in which communities were highly responsive to disturbance (Joyce, 1998; Berg et al., 2012). Therefore, recovery time is critical; a rapid recovery of functional traits is likely to help maintain ecosystem functioning even when the rehabilitation of species richness or abundance takes longer.

Wet grassland plant communities and extreme climate impacts

Research into the impacts of extreme climate events on wet grasslands is needed, because the limited studies on ecosystems generally indicate that extreme events can have significant effects on plant community structure, productivity and growth (Kreyling et al., 2008; Arnone et al., 2011). Additionally, extreme climate events can alter phenological timing by reducing or delaying changes in flowering of grassland species (Jentsch et al., 2009; Sherry et al., 2011). However, community responses are complex, and possibly dependent upon abiotic factors, life stage, and

interspecific differences within the same community (Herrero & Zamora, 2014). In some experimental communities under extreme events, primary productivity was not significantly different from control situations (Fay et al., 2003; Kreyling et al., 2008; Jentsch et al., 2011; Walter et al., 2011; Dreesen et al., 2012) or was found to recover to previous levels the following year (White et al., 2000; Arnone et al., 2011). The productivity of nitrogen-fixing legume species, which are important components of ecosystems and common in many wet grasslands, remained stable after sudden increased temperatures (Arnone et al., 2011). However, legumes do appear to significantly moderate the flowering of other grassland species under both extreme drought and precipitation (Jentsch et al., 2009). Studies on keystone components of wet grassland communities, such as dominant grasses, robust sedges or herbs (such as *Sanguisorba officinalis*), or rare species of nature conservation importance, would provide valuable information on community functioning and management in the face of climate change.

Extreme disturbance events may be characterised by rapid changes in environmental conditions, where community thresholds are exceeded and biota is unable to adapt quickly enough to recover. While there is no published research specifically identifying tipping points for wet grasslands in relation to extreme climate events, there is evidence from other communities that changes following extreme events may be irreversible (Holmgren et al., 2001). Following a severe drought in the 1950's, a Mexican Ponderosa pine forest shifted to a Piñon–juniper woodland within less than 5 years, and despite no further severe droughts over subsequent decades there was no return to the original community (Allen & Breshears, 1998). In Australia, open dryland has changed to woodland following high rainfall succeeding El Niño conditions in the 1870's (Holmgren et al., 2001). Joyce (1998) compared two floodplain grassland plant communities with contrasting responses to disturbance regimes. A flood-meadow community with a stable disturbance regime was characterised by competitive, stress-tolerant species with below-ground storage, while an inundation community intensely disturbed by flooding supported limited species richness and ruderals with short life cycles and high potential growth rate (e.g. rhizomes, stolons). The latter environment offers an insight into possible future wet grassland scenarios

under climate extremes, characterised by greater variability and dynamism (Fig. 1). Evidence from Baltic coastal landscapes suggests that wet grasslands from such dynamic hydrological environments respond rapidly to environmental change while diverse communities with more stable hydroperiods show resistance to perturbation (Berg et al., 2012).

Field studies have indicated that extreme precipitation and flood events can have profound impacts on wet grassland community composition. Intense flooding may affect plant distribution along gradients of inundation tolerance. Less flood tolerant species can show reduced distribution for many years following extreme flooding in contrast to more flood tolerant riparian species (Vervuren et al., 2003). However, vegetation abundance on floodplains does not necessarily significantly decrease after extreme flooding (Sparks et al., 1990), although diversity and species turnover can be immediately affected (Ilg et al., 2008). This suggests that stability is determined by long-term processes allowing the community to remain functional through species turnover. Resilience may be enhanced by a higher number of viable seeds from species tolerant to both wet and dry conditions compared to those restricted to aquatic or terrestrial environments (Nielsen et al., 2013) when recovering from extreme or recurrent flooding. Toogood et al. (2008) also recorded high species turnover in the 2 years following major flooding of a wet grassland, with particular increases in less flood tolerant species suggesting a recovery.

Observations of a lag period after extreme climate treatments indicate that effects can continue into at least the following year in prairie and forest communities (Breda & Badeau, 2008; Sherry et al., 2011). Moreover, Sherry et al. (2012) found that increased temperature and precipitation treatments resulted in no significant effects on prairie community structure until the following year. In contrast, community responses were unrelated to time since water levels were raised in a series of wet grasslands in England, instead being significantly correlated with flooding duration, water table, and soil moisture (Toogood & Joyce, 2009). This suggests that for wet grasslands the magnitude and duration of extreme events will both be critical, potentially prompting more rapid responses than those reported from some terrestrial communities. Nevertheless, there is a good case to be made for extended monitoring after an extreme event. Delayed recovery

of dominant species may release other species from competition, which in turn can facilitate longer term community change in dominance (Cavin et al., 2013) and, therefore, diversity. Furthermore, wet grassland communities can be highly variable over time, with up to 50% species turnover in cut or grazed grasslands each year (Toogood & Joyce, 2009). This indicates the inherent complexity of climate impacts on ecosystems and affirms that a more effective definition of extreme climate events is based on climatological statistics rather than ecological effects.

Conclusions

Definitions of extreme climate events tend to overlook the complex nature of ecological systems. This review has highlighted that plant communities respond differently to extreme events, dependent upon community composition, diversity, life stage, and interactions, with traits that may confer resilience and stability (Fig. 3). Thus, it is doubtful whether extreme climate events can be defined by their ecological response. However, functional plant traits can reduce the complexity of communities without losing information regarding important vegetation processes. Typically, research so far has tended to utilise plant biomass, growth or cover, life-form, and some indicator of phenology to measure ecological responses to extreme climates, sometimes in isolation (Table 2). Phenology would seem to be a more sensitive and reliable indicator of climate impacts than other physiological variables such as biomass, cover and growth. Several metrics for assessing reproductive phenology exist that can be used together to provide a more effective measure of plant fitness. For example, flowering and fruiting periods, and seed production, have been used to measure responses to climate events and other disturbance in various plant communities and could provide the basis of a suite of indicator traits for wet grasslands.

Although still limited, there is an increasing scientific literature about the effects of extreme climate events on ecosystems based upon empirical research (Jentsch et al., 2007; Sherry et al., 2007; Arnone et al., 2011; Dreesen et al., 2012). This is beginning to elucidate how communities respond to increases in extreme events, and investigate whether these responses can be predicted using traits, which is

considered to be among the 100 most relevant contemporary ecological questions (Sutherland et al., 2013). However, ecological experiments often apply average and static trend climate effects as treatments (Beier et al., 2012; Thompson et al., 2013), despite the disproportionate effects of extreme events upon ecosystems, and the likelihood that they accelerate climate impacts. Furthermore, plant responses to climate change may lag behind actual changes in mean temperatures by at least 2 years (Braswell et al., 1997; Breda & Badeau 2008). Additionally, it has been suggested that some extreme precipitation experiments have so far been conservative in their design of magnitudinal events, especially as future conditions may exceed current norms (Beier et al., 2012), or they have been unclear as to whether increasing means or extreme variability are the factors under investigation (Reyer et al., 2013). It is, therefore, important to clearly define how extreme climate treatments compare directly to actual events or return periods and ensure that they are at least at the baseline of magnitude or frequency of a known extreme, or to test beyond known conditions (Reyer et al., 2013). Combining multiple traits and extreme climate events experimentally is rare (Jentsch et al., 2011) but mesocosms allow control of specific environmental conditions and species under investigation. Jentsch et al. (2011) demonstrated that it is practical to use mesocosms to manipulate extreme climate events and monitor plant communities via an array of functional traits. However, results from synthetic communities in mesocosms will need to be extrapolated ideally via field trials and monitoring, which is a considerable challenge especially in dynamic wetland environments.

There is a pressing need for more research on wetland functioning and services in relation to climate extremes, especially as climate events that cause excessive disturbance beyond temporal and spatial norms may cause adverse changes (Öquist & Svensson, 1996). This review has indicated that diverse, managed wet grasslands may be a suitable focus because they support important ecosystem and cultural services, and respond to disturbance regimes with distinctive, measurable ecological changes. Many wet grassland plants carry physiological and mechanistic traits to tolerate disturbance regimes, characteristically episodic inundation, cutting and/or grazing, which are not found in fully terrestrial or natural habitats. Wet grassland ecosystems could be used to

mitigate extremes, partly because intense disturbance favours resource capture via short life cycles and rapid growth rates. A trait-based approach is, therefore, pertinent, especially as diverse wet grassland communities may show resilience to extreme events. Plant traits can also be used in restoration or creation schemes to design more robust wet grassland systems, capable of adapting to future climates.

Open Access This article is distributed under the terms of the Creative Commons Attribution License which permits any use, distribution, and reproduction in any medium, provided the original author(s) and the source are credited.

References

- Acreman, M. C., J. R. Blake, D. J. Booker, R. J. Harding, N. Reynard, J. O. Mountford & C. J. Stratford, 2009. A simple framework for evaluating regional wetland ecohydrological response to climate change with case studies from Great Britain. *Ecohydrology* 2: 1–17.
- Allen, C. D. & D. D. Breshears, 1998. Drought-induced shift of a forest–woodland ecotone: rapid landscape response to climate variation. *Proceedings of the National Academy of Sciences* 95: 14839–14842.
- Arnone III, J. A., R. L. Jasoni, J. A. Lucchesi, J. D. Larsen, E. A. Leger, R. A. Sherry, Y. Luo, D. S. Schimel & P. S. J. Verburg, 2011. A climatically extreme year has large impacts on C₄ species in tallgrass prairie ecosystems but only minor effects on species richness and other plant functional groups. *Journal of Ecology* 99: 678–688.
- Antheunis, A. M. & J. T. A. Verhoeven, 2008. Short-term responses of soil nutrient dynamics and herbaceous riverine plant communities to summer inundation. *Wetlands* 28: 232–244.
- Araya, Y. N., J. Silvertown, D. J. Gowing, K. J. McConway, H. P. Linder & G. Midgley, 2010. A fundamental, ecohydrological basis for niche segregation in plant communities. *New Phytologist* 189: 253–258.
- Beier, C., C. Beierkuhnlein, T. Wohlgemuth, J. Penuelas, B. Emmett, C. Körner, H. de Boeck, J. Hesselbjerg Christensen, S. Leuzinger, I. A. Janssens & K. Hansen, 2012. Precipitation manipulation experiments – challenges and recommendations for the future. *Ecology Letters* 15: 899–911.
- Beisner, B. E., D. Haydon & K. L. Cuddington, 2003. Alternative stable states in ecology. *Frontiers in Ecology and the Environment* 1: 376–382.
- Beltman, B., J. H. Willems & S. Güsewell, 2007. Flood events overrule fertiliser effects on biomass production and species richness in riverine grasslands. *Journal of Vegetation Science* 18: 625–634.
- Berg, M., C. B. Joyce & N. Burnside, 2012. Differential responses of abandoned wet grassland plant communities to reinstated cutting management. *Hydrobiologia* 692: 83–97.

- Bertness, M. D. & R. Callaway, 1994. Positive interactions in communities. *Trends in Ecology and Evolution* 9: 191–195.
- Blom, C. W. P. M. & L. A. C. J. Voeseenek, 1996. Flooding: the survival strategies of plants. *Trends in Ecology and Evolution* 11: 290–295.
- Boutin, C. & P. A. Keddy, 1993. A functional classification of wetland plants. *Journal of Vegetation Science* 4: 591–600.
- Braswell, B. H., D. S. Schimel, E. Linder & B. Moore III, 1997. The response of global terrestrial ecosystems to interannual temperature variability. *Science* 278: 870–872.
- Breda, N. & V. Badeau, 2008. Forest tree responses to extreme drought and some biotic events: Towards a selection according to hazard tolerance? *External Geophysics, Climate and Environment* 34(0): 651–662.
- Brinson, M. M. & A. I. Malvárez, 2002. Temperate freshwater wetlands: types, status, and threats. *Environmental Conservation* 29(2): 115–133.
- Brooker, R. W., F. T. Maestre, R. M. Callaway, C. L. Lortie, L. A. Cavieres, G. Kunstler, P. Laincourt, K. Tielborger, J. M. J. Travis, F. Anthelme, C. Armas, L. Coll, E. Corcket, S. Delzon, E. Forey, Z. Kikvidze, J. Olofsson, F. Pugnaire, C. L. Quiroz, P. Saccone, K. Schiffers, M. Seifan, B. Touzard & R. Michalet, 2008. Facilitation in plant communities: the past, the present, and the future. *Journal of Ecology* 96: 18–34.
- Burgess, N. D., C. E. Evans & G. J. Thomas, 1990. Vegetation change on the Ouse Washes wetland, England, 1972–88 and effects on their conservation importance. *Biological Conservation* 53: 173–189.
- Butterfield, B. J. & K. N. Suding, 2013. Single-trait functional indices outperform multi-trait indices in linking environmental gradients and ecosystem services in a complex landscape. *Journal of Ecology* 101: 9–17.
- Byun, C., S. de Blois & J. Brisson, 2013. Plant functional group identity and diversity determine biotic resistance to invasion by an exotic grass. *Journal of Ecology* 101: 128–139.
- Cadotte, M. W., J. Cavender-Bares, D. Tilman & T. H. Oakley, 2009. Using phylogenetic, functional and trait diversity to understand patterns of plant community productivity. *PLoS One* 4: e5695.
- Cadotte, M. W., K. Carscadden & N. Mirotchnick, 2011. Beyond species: functional diversity and the maintenance of ecological processes and services. *Journal of Applied Ecology* 48: 1079–1087.
- Cardinale, B. J., J. P. Wright, M. W. Cadotte, I. T. Carroll, A. Hector, D. S. Srivastava, M. Loreau & J. J. Weis, 2007. Impacts of plant diversity on biomass production increase through time because of species complementarity. *Proceedings of the National Academy of Sciences* 104: 18123–18128.
- Cavin, L., E. P. Mountford, G. F. Peterken & A. S. Jump, 2013. Extreme drought alters competitive dominance within and between tree species in a mixed forest stand. *Functional Ecology* 27: 1424–1435.
- Čížková, H., J. Květ, F. A. Comín, R. Laiho, J. Pokorný & D. Pithart, 2013. Actual state of European wetlands and their possible future in the context of global climate change. *Aquatic Sciences* 75: 3–26.
- Dawson, T. P., P. M. Berry & E. Kampa, 2003. Climate change impacts on freshwater wetland habitats. *Journal for Nature Conservation* 11: 25–30.
- De Boeck, H. J., F. E. Dreesen, I. A. Janssens & I. Nijs, 2011. Whole-system responses of experimental plant communities to climate extremes imposed in different seasons. *New Phytologist* 189: 806–817.
- Díaz, S. & M. Cabido, 2001. Vive la différence: plant functional diversity matters to ecosystem processes. *Trends in Ecology and Evolution* 16: 646–655.
- Díaz, S., J. G. Hodgson, K. Thompson, M. Cabido, J. H. C. Cornelissen, A. Jalili, G. Montserrat-Martí, J. P. Grime, F. Zarrinkamar, Y. Asri, S. R. Band, S. Basconcelo, P. Castro-Díez, G. Fumes, B. Hamzehee, M. Khoshnevi, M. C. Pérez-Romtomé, F. A. Shirvany, S. Yazdani, R. Abbas-Azimi, A. Bogaard, S. Boustani, M. Charles, M. Dehghan, L. de Torres-Espuny, V. Falczuk, J. Guerrero-Campo, A. Hynd, G. Jones, E. Kowsary, F. Kazemi-Saeed, M. Maestro-Martínez, A. Romo-Díez, S. Shaw, B. Siavash, P. Villar-Salvador & M. R. Zak, 2004. The plant traits that drive ecosystems: evidence from three continents. *Journal of Vegetation Science* 15: 295–304.
- Díaz, S., J. Fargione, F. S. Chapin III & D. Tilman, 2006. Biodiversity loss threatens human well-being. *PLoS, Biology* 4: 1300–1305.
- Díaz, S., S. Lavorel, F. de Bello, F. Quéfier, K. Grigulis & T. M. Robson, 2007. Incorporating plant functional diversity effects in ecosystem service assessments. *Proceedings of the National Academy of Sciences* 104: 20684–20689.
- Dreesen, F. E., H. J. De Boeck, I. A. Janssens & I. Nijs, 2012. Summer heat and drought extremes trigger unexpected changes in productivity of a temperate annual/biannual plant community. *Environmental and Experimental Botany* 79: 21–30.
- Dreesen, F. E., H. J. De Boeck, I. A. Janssens & I. Nijs, 2013. Do successive climate extremes weaken the resistance of plant communities? An experimental study using plant assemblages. *Biogeosciences Discussions* 10: 9149–9177.
- Easterling, D. R., G. A. Meehl, C. Parmesan, S. A. Changnon, T. R. Karl & L. O. Mearns, 2000. Climate extremes: observations, modelling, and impacts. *Science* 289: 2068–2074.
- Eliáš Jr., P., D. Sopotlieva, D. Dítě, P. Hájková, I. Apostolova, D. Senko, Z. Melečková & M. Hájek, 2013. Vegetation diversity of salt-rich grasslands in Southeast Europe. *Applied Vegetation Science* 16: 521–537.
- Erwin, K. L., 2009. Wetlands and global climate change: the role of wetland restoration in a changing world. *Wetlands Ecology and Management* 17: 71–84.
- Fay, P. A., J. D. Carlisle, A. K. Knapp, J. M. Blair & S. L. Collins, 2003. Productivity responses to altered rainfall patterns in a C₄-dominated grassland. *Oecologia* 137: 245–251.
- Fowler, H. J. & R. L. Wilby, 2010. Detecting changes in seasonal precipitation extremes using regional climate model projections: implications for managing fluvial flood risk. *Water Resources Research*. doi:10.1029/2008WR007636.
- Gibson, D. J., S. G. Baer, R. P. Klopff, L. K. Reed, B. R. Wodika & J. E. Willand, 2013. Limited effects of dominant species population source on community composition during community assembly. *Journal of Vegetation Science* 24: 429–440.
- Gitay H, Finlayson C M & Davidson N, 2011. A framework for assessing the vulnerability of wetlands to climate change, Ramsar Technical Report No. 5/CBD Technical Series No. 57, Ramsar Convention Secretariat, Gland & Secretariat of the Convention on Biological Diversity, Montreal.

- Grime, J. P., 1979. *Plant Strategies and Vegetation Processes*. Wiley, Chichester.
- Grime, J. P., 1998. Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *Journal of Ecology* 86: 902–910.
- Grimm, V. & C. Wissel, 1997. Babel, or the ecological stability discussions: an inventory and analysis of terminology and a guide for avoiding confusion. *Oecologia* 109: 323–334.
- Gutschick, V. P. & H. BassiriRad, 2003. Extreme events as shaping physiology, ecology, and evolution of plants: toward a unified definition and evaluation of their consequences. *New Phytologist* 160: 21–42.
- Herrero, A. & R. Zamora, 2014. Plant responses to extreme climatic events: a field test of resilience capacity at the southern range edge. *PLoS One* 9: e87842.
- Holmgren, M., M. Scheffer, E. Ezcurra, J. R. Gutiérrez & G. M. J. Mohren, 2001. El Niño effects on the dynamics of terrestrial ecosystems. *Trends in Ecology and Evolution* 16: 89–94.
- Hooper, D. U., F. S. Chapin III, J. J. Ewel, A. Hector, P. Inchausti, S. Lavorel, J. H. Lawton, D. M. Lodge, M. Loreau, S. Naeem, B. Schmid, H. Setälä, A. J. Symstad, J. Vandermeer & D. A. Wardle, 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs* 75: 3–35.
- Ilg, C., F. Dziock, F. Fockler, K. Follner, M. Gerisch, J. Glaeser, A. Rink, A. Schanowski, M. Scholz, O. Deichner & K. Henle, 2008. Long-term reactions of plants and macroinvertebrates to extreme floods in floodplain grasslands. *Ecology* 89: 2392–2398.
- IPCC, 2007. *Climate Change 2007: The physical science basis, Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge.
- IPCC, 2012. *Summary for Policymakers*. In Field C B et al (eds), *Managing the Risks of Extreme Events and Disasters to Advance Climate Change Adaptation, A Special Report of Working Groups I and II of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge.
- IPCC, 2013. *Working Group I Contribution to the IPCC Fifth Assessment Report Climate Change 2013: The Physical Science Basis Summary for Policymakers*. Cambridge University Press, Cambridge.
- IPCC, 2014. *Climate Change 2014: Impacts, Adaptations and Vulnerability. Summary for Policymakers*. Cambridge University Press, Cambridge.
- Isbell, F., V. Calcagno, A. Hector, J. Connolly, W. S. Harpole, P. B. Reich, M. Scherer-Lorenzen, B. Schmid, D. Tilman, J. van Ruijven, A. Weigelt, B. J. Wilsey, E. S. Zavaleta & M. Loreau, 2011. High plant diversity is needed to maintain ecosystem services. *Nature* 477: 199–203.
- Jentsch, A., J. Kreyling & C. Beierkuhnlein, 2007. A new generation of climate-change experiments: events, not trends. *Frontiers in Ecology and the Environment* 5: 365–374.
- Jentsch, A., J. Kreyling, J. Boettcher-Treschkow & C. Beierkuhnlein, 2009. Beyond gradual warming: extreme weather events alter flower phenology of European grassland and heath species. *Global Change Biology* 15: 837–849.
- Jentsch, A., J. Kreyling, M. Elmer, E. Gellesch, B. Glaser, K. Grant, R. Hein, M. Lara, H. Mirzae, S. E. Nadler, L. Nagy, D. Otieno, K. Pritsch, U. Rascher, M. Schädler, M. Schloter, B. K. Singh, J. Stadler, J. Walter, C. Wellstein, J. Wöllecke & C. Beierkuhnlein, 2011. Climate extremes initiate ecosystem-regulating functions while maintaining productivity. *Journal of Ecology* 99: 689–702.
- Joyce, C. B., 1998. Plant community dynamics of managed and unmanaged floodplain grasslands: an ordination analysis. In Joyce, C. B. & P. M. Wade (eds), *European Wet Grasslands: Biodiversity, Management and Restoration*. Wiley, Chichester: 173–191.
- Joyce, C. B., 2001. The sensitivity of a species-rich flood-meadow plant community to fertilizer nitrogen: the Lužnice river floodplain, Czech Republic. *Plant Ecology* 155: 47–60.
- Joyce, C. B., 2014. Ecological consequences and restoration potential of abandoned wet grasslands. *Ecological Engineering* 66: 91–102.
- Joyce, C. B. & P. M. Wade, 1998. Wet grasslands: a European perspective. In Joyce, C. B. & P. M. Wade (eds), *European Wet Grasslands: Biodiversity, Management and Restoration*. Wiley, Chichester: 1–11.
- Koyama, A. & S. Tsuyuzaki, 2013. Facilitation by tussock-forming species on seedling establishment collapses in an extreme drought year in a post-mined *Sphagnum* peatland. *Journal of Vegetation Science* 24: 473–483.
- Kreyling, J., M. Wenigmann, C. Beierkuhnlein & A. Jentsch, 2008. Effects of extreme weather events on plant productivity and tissue die-back are modified by community composition. *Ecosystems* 11: 752–763.
- Kundzewicz, Z. W., U. Ulbrich, T. Brücher, D. Graczyk, A. Krüger, G. Leckebusch, L. Menzel, I. Pińskwar, M. Radziejewski & M. Szwed, 2005. Summer floods in central Europe – Climate change track? *Natural Hazards* 36: 165–189.
- Lavorel, S. & E. Garnier, 2002. Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Functional Ecology* 16: 545–556.
- Lavorel, S., S. Díaz, J. Hans, C. Cornelissen, E. Garnier, S. P. Harrison, S. McIntyre, J. G. Pausas, N. Pérez-Harguindeguy, C. Roumet & C. Urcelay, 2007. Plant functional types: Are we getting any closer to the Holy Grail? In Canadell, J. G., D. E. DE Pataki & L. F. Pitelka (eds), *Terrestrial Ecosystems in a Changing World*. Springer, Berlin: 149–159.
- Lloret, F. & I. Granzow-de la Cerda, 2013. Plant competition and facilitation after extreme drought episodes in Mediterranean shrubland: Does damage to vegetation cover trigger replacement by juniper woodland? *Journal of Vegetation Science* 24: 1020–1032.
- Lloret, F., D. Siscart & C. Dalmases, 2004. Canopy recovery after drought dieback in holm-oak Mediterranean forests of Catalonia (NE Spain). *Global Change Biology* 10: 2092–2099.
- Loreau, M., 2000. Biodiversity and ecosystem functioning: recent theoretical advances. *Oikos* 91: 3–17.
- Loreau, M. & N. Behera, 1999. Phenotypic diversity and stability of ecosystem processes. *Theoretical Population Biology* 56: 29–47.
- Loreau, M., S. Naeem, P. Inchausti, J. Bengtsson, J. P. Grime, A. Hector, D. U. Hooper, M. A. Huston, D. Raffaelli, B.

- Schmid, D. Tilman & D. A. Wardle, 2001. Biodiversity and ecosystem functioning: current knowledge and future challenges. *Science* 294: 804–808.
- McCarty, J. P., 2001. Ecological Consequences of recent climate change. *Conservation Biology* 15: 320–331.
- Meehl, G. A., T. Karl, D. R. Easterling, S. Changnon, R. Pielke Jr, D. Changnon, J. Evans, P. Y. Groisman, T. R. Knutson, K. E. Kunkel, L. O. Mearns, C. Parmesan, R. Pulwarty, T. Root, R. T. Sylves, P. Whetton & F. Zwiers, 2000. An introduction to trends in extreme weather and climate events: observations, socioeconomic impacts, terrestrial ecological impacts, and model projections. *Bulletin of the American Meteorological Society* 81: 413–416.
- Milly, P. C. D., R. T. Wetherald, K. A. Dunne & T. L. Delworth, 2002. Increasing risk of great floods in a changing climate. *Nature* 415: 514–517.
- Mori, A. S., 2011. Ecosystem management based on natural disturbances: hierarchical context and non-equilibrium paradigm. *Journal of Applied Ecology* 48: 280–292.
- Nielsen, D. L., K. Podnar, R. J. Watts & A. L. Wilson, 2013. Empirical evidence linking increased hydrologic stability with decreased biotic diversity within wetlands. *Hydrobiologia* 708: 81–96.
- Niu, S., Y. Luo, D. Li, S. Cao, J. Xia, J. Li & M. D. Smith, 2014. Plant growth and mortality under climatic extremes: an overview. *Environmental and Experimental Botany* 98: 13–19.
- Norberg, J., 2004. Biodiversity and ecosystem functioning: a complex adaptive systems approach. *Limnology and Oceanography* 49: 1269–1277.
- O’Gorman, E. J. & M. C. Emmerson, 2009. Perturbations to trophic interactions and the stability of complex food webs. *Proceedings of the National Academy of Sciences* 106: 13393–13398.
- O’Gorman, P. A. & T. Schneider, 2009a. Scaling of precipitation extremes over a wide range of climates simulated with an idealized GCM. *Journal of Climate* 22: 5676–5686.
- O’Gorman, P. A. & T. Schneider, 2009b. The physical basis for increases in precipitation extremes in simulations of 21st-century climate change. *Proceedings of the National Academy of Sciences* 106: 14773–14777.
- Orlowsky, B. & S. I. Seneviratne, 2012. Global changes in extreme events: regional and seasonal dimension. *Climatic Change* 110: 669–696.
- Öquist, M. G. & B. H. Svensson, 1996. Non-tidal wetlands. In Watson, T. R., M. C. Zinyowera & R. H. Moss (eds), *Climate Change 1995: Impacts, Adaptations and Mitigation of Climate Change: Scientific-Technical Analyses. Contribution of Working Group II to the Second Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge: 215–239.
- Peñuelas, J., C. Gordon, L. Llorens, T. Nielsen, A. Tietema, C. Beier, P. Bruna, B. Emmett, M. Estiarte & A. Gorissen, 2004. Noninvasive field experiments show different plant responses to warming and drought among sites, seasons, and species in a north–south European gradient. *Ecosystems* 7: 598–612.
- Planton, S., M. Déqué, F. Chauvin & L. Terray, 2008. Expected impacts of climate change on extreme climate events. *Geoscience* 340: 564–574.
- Ramsar, 2002. Climate change and wetlands: impacts, adaptation and mitigation, at ‘Wetlands: water, life, and culture’. In 8th Meeting of the Conference of the Contracting Parties to the Convention on Wetlands (Ramsar, Iran, 1971) Valencia: 18–26.
- Reusch, T. B. H., A. Ehlers, A. Hämmerli & B. Worm, 2005. Ecosystem recovery after climatic extremes enhanced by genotypic diversity. *Proceedings of the National Academy of Sciences* 102: 2826–2831.
- Reyer, C. P. O., S. Leuzinger, A. Rammig, A. Wolf, R. P. Bartholomeus, A. Bonfante, F. De Lorenzi, M. Dury, P. Gloning, R. A. Jaoué, T. Klein, T. M. Kuster, M. Martins, G. Niedrist, M. Riccardi, G. Wohlfahrt, P. De Angelis, G. De Dato, L. François, A. Menzel & M. Pereira, 2013. A plant’s perspective of extremes: terrestrial plant responses to changing climatic variability. *Global Change Biology* 19: 75–89.
- Sherry, R. A., X. Zhou, S. Gu, J. A. Arnone, D. S. Schimel, P. S. Verburg, L. L. Wallace & Y. Luo, 2007. Divergence of reproductive phenology under climate warming. *Proceedings of the National Academy of Sciences* 104: 198–202.
- Sherry, R. A., X. Zhou, S. Gu, J. A. Arnone, D. W. Johnson, D. S. Schimel, P. S. J. Verburg, L. L. Wallace & Y. Luo, 2011. Changes in duration of reproductive phases and lagged phenological response to experimental climate warming. *Plant Ecology and Diversity* 4: 23–35.
- Sherry, R. A., J. A. Arnone III, D. W. Johnson, D. S. Schimel, P. S. Verburg & Y. Luo, 2012. Carry over from previous year environmental conditions alters dominance hierarchy in a prairie plant community. *Journal of Plant Ecology* 5: 134–146.
- Smith, C., 2011a. An ecological perspective on extreme climatic events: a synthetic definition and framework to guide future research. *Journal of Ecology* 99: 656–663.
- Smith, C., 2011b. The ecological role of climate extremes: current understanding and future prospects. *Journal of Ecology* 99: 651–655.
- Sparks, R. E., P. B. Bayley, S. L. Kohler & L. L. Osborne, 1990. Disturbance and recovery of large floodplain rivers. *Environmental Management* 14: 699–709.
- Steddel, B., Y. Hautier, A. Hector & M. Kessler, 2011. Diverse marsh plant communities are more consistently productive across a range of different environmental conditions through functional complementarity. *Journal of Applied Ecology* 48: 1117–1124.
- Sutherland, W. J., R. P. Freckleton, H. C. J. Godfray, S. R. Beissinger, T. Benton, D. D. Cameron, Y. Carmel, D. A. Coomes, T. Coulson, M. C. Emmerson, R. S. Hails, G. C. Hays, D. J. Hodgson, M. J. Hutchings, D. Johnson, J. P. G. Jones, M. J. Keeling, H. Kokko, W. E. Kunin, X. Lambin, O. T. Lewis, Y. Malhi, N. Mieszkowska, E. J. Milner-Gulland, K. Norris, A. B. Phillimore, D. W. Purves, J. M. Reid, D. C. Reuman, K. Thompson, J. M. J. Travis, L. A. Turnbull, D. A. Wardle & T. Wiegand, 2013. Identification of 100 fundamental ecological questions. *Journal of Ecology* 101: 58–67.
- Tebaldi, C., K. Hayhoe, J. Arblaster & G. A. Meehl, 2006. Going to extremes: the intercomparison of model-simulated historical and future changes in extreme events. *Climatic Change* 79: 185–211.

- Thompson, J. R., H. Gavin, A. Refsgaard, R. H. Sørensen & D. J. Gowing, 2009. Modelling the hydrological impacts of climate change on UK lowland wet grassland. *Wetlands Ecology and Management* 17: 503–523.
- Thompson, R. M., J. Beardall, J. Beringer, M. Grace & P. Sardina, 2013. Means and extremes: building variability into community-level climate change experiments. *Ecology Letters* 16: 799–806.
- Toogood, S. E. & C. B. Joyce, 2009. Effects of raised water levels on wet grassland plant communities. *Applied Vegetation Science* 12: 283–294.
- Toogood, S. E., C. B. Joyce & S. Waite, 2008. Response of floodplain grassland plant communities to altered water regimes. *Plant Ecology* 197: 285–298.
- Trenberth, K. E. & J. T. Fasullo, 2012. Climate extremes and climate change: the Russian heat wave and other climate extremes of 2010. *Journal of Geophysical Research* 117: D17103.
- Valladares, F. & Ü. Niinemets, 2008. Shade tolerance, a key plant trait of complex nature and consequences. *Annual Review of Ecology, Systematics and Evolution* 39: 237–257.
- Vervuren, P. J. A., C. W. P. M. Blom & H. de Kroon, 2003. Extreme flooding events on the Rhine and the survival and distribution of riparian plant species. *Journal of Ecology* 91: 135–146.
- Violle, C., M. Navas, D. Vile, E. Kazakou, C. Fortunel, I. Hummel & E. Garnier, 2007. Let the concept of trait be functional! *Oikos* 116: 882–892.
- Walter, J., L. Nagy, R. Hein, U. Rascher, C. Beierkuhnlein, E. Willner & A. Jentsch, 2011. Do plants remember drought? Hints towards a drought-memory in grasses. *Environmental and Experimental Botany* 71: 34–40.
- Walter, J., A. Jentsch, C. Beierkuhnlein & J. Kreyling, 2013. Ecological stress memory and cross stress tolerance in plants in the face of climate extremes. *Environmental and Experimental Botany* 94: 3–8.
- Weihner, E., A. van der Werf, K. Thompson, M. Roderick, E. Garnier & O. Eriksson, 1999. Challenging Theophrastus: a common core list of plant traits for functional ecology. *Journal of Vegetation Science* 10: 609–620.
- White, T. A., B. D. Campbell, P. D. Kemp & C. L. Hunt, 2000. Sensitivity of three grassland communities to simulated extreme temperature and rainfall events. *Global Change Biology* 6: 671–684.
- Zhang, L. & H. Shao, 2013. Direct plant–plant facilitation in coastal wetlands: a review. *Estuarine, Coastal and Shelf Science* 119: 1–6.
- Zwiers, F. W. & V. V. Khari, 1998. Changes in the extremes of the climate simulated by CCC GCM2 under CO₂ doubling. *Journal of Climate* 11: 2200–2222.